EASTERN ASIAN–EASTERN NORTH AMERICAN FLORISTIC RELATIONS: THE PLANT COMMUNITY LEVEL

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ABSTRACT

Most comparisons of the temperate floras of eastern North America and eastern Asia have addressed the systematic or floristic level. Data on vegetation pattern and structure, when present, have been broadly descriptive, with little detail on gradient relations or intercommunity pattern. Great Smoky Mountains National Park, the largest eastern temperate preserve of floristic diversity in the United States, lies near the center of development of the North American deciduous forest. The flora of this park was used to model the gradient distributions and ecological characteristics of species with east Asian near-relatives. The disjunct taxa (162 species or 13 percent of the flora) were a highly non-random assortment of the native flora (total = 1,211 species) as a whole: they were more likely to be primitive in phylogenetic standing, perennial, and woody. They were also non-randomly distributed among habitats, being more likely to be found on exclusively terrestrial, forested, and mesic sites. Taxa belonging to genera absent from eastern Asia (232 species or 19 percent of the flora) were an equally interesting non-random sample of the native flora: they were more likely to be herbaceous and advanced in phylogenetic standing. Absent taxa, however, essentially represented a random sample of the flora as a whole in terms of degree of habitat openness and substrate type. When gradient distributions were corrected for overall species richness distributions, absent taxa showed their peak importance on xeric sites. Taxa in wide-ranging north temperate genera (817 species or 67 percent of the flora) generally constituted a random sample of the flora as a whole; they showed peak importance at higher elevations. These data are used to make inferences about the distribution of species richness in the Smokies landscape. Evidence that the eastern Asian temperate deciduous forests were the most diverse temperate forests on earth is also reviewed. Alternative hypotheses concerning the nature of this heightened diversity are discussed.

Investigations of the floristic relationship between temperate eastern Asia and eastern North America generally have treated such relationships at the geographical, systematic, or evolutionary level. There are, however, important ecological correlates to this relationship that have gone, for the most part, untested. This investigation uses a well-known eastern North American landscape, the Great Smoky Mountains, to examine ecological correlates of the floristic relationship. Although others have qualitatively described many of these patterns (cf. Hu, 1936; Cain, 1943; Li, 1952; Wang, 1961), quantitative studies have been lacking. An objective of this research, then, was to develop explicit tests for the distribution of ecological properties in the flora as a function of phytogeography. The landscape distribution of the Great Smoky Mountains flora was used to develop and discuss community level hypotheses on the eastern Asian–North American floristic relationship.

NORTH TEMPERATE DISJUNCTION AND DIVERSITY

The disjunctions between eastern Asia and eastern North American are generally at the generic level, although a few plants are conspecific and others are disjunct only at subfamily or subgeneric levels (Good, 1927; Li, 1952, 1972; Sharp, 1953; Graham, 1972; Wood, 1970, 1972; see also other papers, this volume). About 13 percent of the genera in the southeastern United States is involved (Wood, 1972). Some 62 genera are strictly disjunct; another 58 genera are nearly so, being strongly discontinuous in their range (Wood, 1972; Li, 1952). There are an additional 37 disjunctions at subgeneric and subfamily levels (Li, 1952, 1972; Wood, 1972). These disjunctions probably developed under the combined influence of continental drift, increasing aridity, and climatic cooling during the last 50–75 million years. These events caused fragmentation of the Arcto-Tertiary geoflora, the most diverse remnants of which now dominate the eastern sides of the north temperate continents. Late Cenozoic extinctions were a final factor in the pattern now observed; these were less important in eastern Asia than in eastern North America and less important in the latter area than in other Arcto-Tertiary centers (e.g., Europe and northwestern North America).

The ecological parallels between eastern Asia

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TABLE 1. Diversity ratios for the genera and families of eastern Asian–eastern North American disjunct vascular plants (data calculated from Li, 1952).

Diversity Ratio	n	Eastern Asia	Eastern North America
Genera/family	23	3.6	2.4
Species/genus:			
Temperate genera	37	2.7	1.9
Temperate-tropical genera	19	13.8	3.2
All genera	56	6.5	2.3
Species/family	23	23.4	5.5

and eastern North America have been studied to a lesser extent, but are also intriguing: 1) woody, broad-leaved, deciduous plants are prominent in the disjunct groups and dominate the forested landscapes of both areas (Li, 1952; Wang, 1961; Wood, 1972); 2) disjunct herbaceous taxa tend to be rhizomatous or tuberous, spring-blooming, early-leafing ephemerals or shade-adapted geophytes (Li, 1952); 3) broad-scale generic turnover along environmental gradients is similar in the two areas (for example, both areas have *Quercus-Acer-Betula-Picea* south-to-north latitudinal gradients (Wang, 1961; Braun, 1950); and 4) overall climatic regimes also are similar (e.g., precipitation is available year round). The similarities in life history and physiognomy are presumably the result of descent from common ancestors that has taken place in similar environments (Li, 1972) rather than the result of convergence *because* of similar environments. Nonetheless, these functional parallels have apparently survived some 50 million years of isolation, taxonomic divergence at the specific level, and episodes of worldwide climatic change. Li (1952) also noted phylogenetic correlates to the disjunctions: Ranalian families are prominent in the list of disjunct groups.

By far the most important observation at the community level is the comparative species richness of the various remnants of the Arcto-Tertiary flora. Most of the disjunct genera have more species in eastern Asia than in eastern North America (Li, 1952; Table 1). In addition, the families with disjunct genera in both areas often have more total genera in eastern Asia than in eastern North America. The result is that there are over four times as many species in the disjunct groups in eastern Asia (Table 1). In addition, temperate Asian families and genera that presently are not native in eastern North America are known from the fossil record there (notably *Ginkgo, Metasequoia, Cercidiphyllum, Dipteronia, Pterocarya,* and *Zelkova*; Axelrod, 1984). These same statements apply to the contrast between eastern North America and Europe: North America is richer in deciduous forest taxa than is Europe and some of the presently disjunct American-Asian taxa are known as fossils in Europe (Wood 1970; Axelrod, 1984). The differences in floristic richness among eastern Asia, North America, and Europe probably results from differing Pleistocene extinction rates in the three areas. Prior to the advent of man, eastern Asia harbored the world's most diverse temperate forests.

We should be cautious in accepting this apparently higher species richness in eastern Asia, however. Although disjunct groups are more diverse in eastern Asia, other non-disjunct groups can be richer in North America (for example, this seems to be true in Asteraceae). Communities from the two continents must be carefully compared. For example, Wang (1961) used the term "mixed mesophytic" forest in China for the rich mixed evergreen-deciduous forests of southerly latitudes. The "mixed-mesophytic" forest of eastern North America is almost entirely deciduous (Braun, 1950). Further, eastern Asia has a much more complete and complex temperate to tropical gradient on mesic sites (this is a gradient of increasing species richness); the gradient in eastern North America is interrupted by the coastal plain and Gulf of Mexico. Finally, there might also be differences in taxonomic treatment in the two areas. Despite these caveats, some of the increased richness in eastern Asia is hardly debatable (e.g., the striped-bark maples, *Acer* sect. *Macrantha* or the distinctive endemic Asian genera already noted).

If the heightened species richness is real, its resolution is fundamental to community level comparisons between eastern Asia and eastern North America. How is the added species richness partitioned in the landscape? There are three possibilities (Whittaker, 1972): 1) higher alpha diversity (within-community species packing or point diversity); 2) higher beta diversity (closer species packing along gradients); and 3) higher gamma diversity (closer species packing across whole landscapes). Three kinds of gamma diversity are: a) that caused by different habitat diversities within one landscape; b) that caused by the interplay of natural disturbance and

succession (White, 1979); and c) that caused by geographic isolation and allopatric speciation (i.e., the development of sibling species across geographic barriers).

At present, a complete resolution of these questions is impossible: quantitative data on Chinese forests are scarce. There is some question whether a resolution will ever be possible: that country has been under intense pressures of population growth for centuries (Smil, 1981) and has only recently formulated conservation policies (Wang, 1980).

This paper, then, addresses these questions through an analysis of one relatively well-known eastern North American landscape, the Great Smoky Mountains, in North Carolina and Tennessee, which lies near the center of diversity of the eastern deciduous forest (Braun, 1950; Whittaker, 1956; Monk, 1967). I examined the community level using two aspects of the flora of this region: autecology (how the plants behave—their life history, growth form, gradient distribution), and synecology (here, the diversity patterns of the plant communities). Ecological properties of the flora were modelled as a function of phytogeographical category. Primary questions were: Are the disjunct taxa a random assortment of the life histories and growth forms of the flora as a whole? Are the disjunct taxa randomly distributed in the Smokies landscape? How is species richness distributed in the landscape? Although many of the questions had been qualitatively addressed previously (see Li, 1952; Cain, 1943), they previously had not been tested explicitly against appropriate random models.

THE STUDY AREA: THE GREAT SMOKY MOUNTAINS

Great Smoky Mountains National Park (hereafter, GRSM: 208,000 ha) is the largest United States National Park in a deciduous forest landscape. It is located at 35°30'N latitude in the southern Appalachian Mountains (Fig. 1), near the richest part of the deciduous forest (Braun, 1950; Monk, 1967). Elevation ranges from 260 to 2,021 m. The climate is continental: July temperature averages 22°C at 445 m and 13.5°C at 1,920 m; January temperature averages 4.5°C at 445 m and −0.8°C at 1,920 m (Shanks, 1954). Precipitation averages 147 cm at 445 m and 231 cm at 1,920 m. Deciduous forest is dominant on mesic to subxeric sites below 1,900 m. Spruce-fir evergreen needle-leaved forest is dominant

above this elevation. Pine forest dominates the driest sites at low and mid elevations and hemlock dominates cool stream valleys (Whittaker, 1956). The mountains are not high enough for a climatic tree line, but two kinds of tree-less communities (grassy balds and heath balds) occur; these are probably a result of disturbance and/ or exposure.

METHODS

The 1,211 native vascular plants of Great Smoky Mountains National Park (White, 1982) are divided into three phytogeographical categories (this is usually done at the generic level— see Wood, 1972): 1) taxa strictly disjunct (e.g., *Caulophyllum*) or strongly discontinuous (e.g., *Aesculus*), found in eastern Asia, eastern North America, and occasionally in one or two other Arcto-Tertiary refuges (e.g., Pacific northwestern North America and mountainous southeastern Europe); 2) genera widely distributed in the North Temperate zone (e.g., *Quercus*); and 3) North American genera absent from eastern Asia (e.g., *Phacelia*). There is continuous gradation from disjunct to discontinuous to wide-ranging genera; for disjunct taxa, the floristic judgments of Wood (1970, 1972) and Li (1952, 1972) are followed.

All plants were coded for a series of autecological characteristics: life history, growth form, deciduousness, height when mature, life form (Raunkiaer, 1934), and phenology. Community data developed through a vegetation monitoring program and distribution data organized through computerization of herbarium labels were used to code presence of the plant species along three dominant environmental gradients: 1) elevation, 2) site moisture class (hydric, mesic, submesic-subxeric, xeric), and 3) relationship to disturbance and succession (habitat coded as: full sun, partial shade, and full shade). These three gradients are strongly correlated with plant distribution in the southern Appalachians (Whittaker, 1956; Golden, 1974).

Species richness within communites (alpha diversity) and along gradients (beta diversity) was derived from the distributional data described above. These data were also used for gauging the effect of disturbance patches on species richness. Landscape (gamma) diversity was approached using an analysis of plant abundance and distribution; all species were coded for abundance and evenness of distribution throughout the park
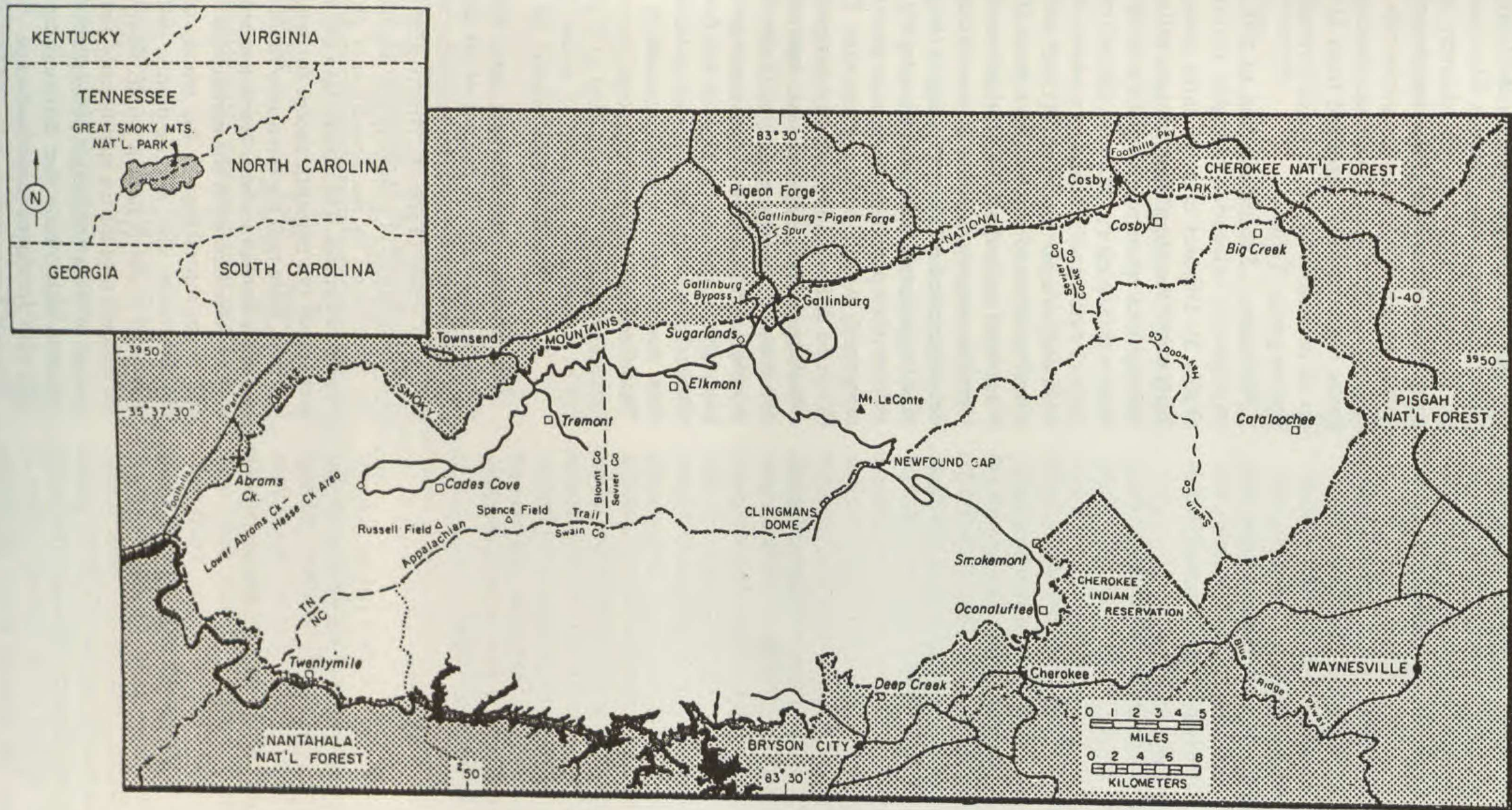
FIGURE 1.   Location of Great Smoky Mountains National Park, North Carolina and Tennessee.

(both taken from White, 1982). Only species richness was analyzed; dominance relations of species within communities were not addressed.

Finally, a phylogenetic code was developed to test the distribution of taxa by presumed distance from the Ranales. Higher groups were assigned to three categories (Stebbins, 1974): 1) Primitive—Superorders Magnoliidae and Alismatidae; 2) Intermediate—Superorders Rosidae, Hamamelidae, Dilleniidae, and Caryophyllidae, and Orders Liliales, Commelinales, and Juncales; and 3) Advanced—Superorder Asteridae, and Orders Orchidales, Cyperales, and Poales.

Plants in the three phytogeographical categories were contrasted with the total native flora for each of the phylogenetic, natural history, and habitat variables. The null hypothesis in each case was that the plants in the separate geographical categories represented a random sample of the flora as a whole; the probability level of 0.05 was used as the criterion of significance. The data were analyzed in two ways: 1) percent distribution of ecological attributes within phytogeographical categories (i.e., normalizing to a common species pool, 100 taxa, within each category); and 2) percent distribution of phytogeographical categories within each ecological characteristic (i.e., percent contribution of each floristic category to a particular ecological category. In the former case, the spectrum of ecological characteristics within a phytogeographical category was compared to that spectrum in the flora as a whole; in the latter case, the percent contribution of the floristic category to a particular ecological category was compared to its percent contribution to the flora as a whole. Statistical analysis and graphic presentation were done at the University of Tennessee Computing Center.

RESULTS

Thirteen percent of GRSM's native vascular plants belong to genera that are disjunct or discontinuous (hereafter called "disjunct" plants); 19 percent belong to genera that are absent from eastern Asia (hereafter "absent" plants); and 68 percent belong to genera with wide north temperate distributions (hereafter "no. temperate" plants) (Table 2). Because the latter group of plants also occurs in eastern Asia, 81 percent of the GRSM flora belong to genera that occur in eastern Asia. Twenty-five percent of GRSM genera are in the disjunct category; these genera account for about 60 percent of the disjunct genera of Wood (1972). The disjunct genera are poorer

(average = 1.5) in species than the total native genera (average = 2.8) (Table 2). The absent genera (average = 1.9) also are relatively species-poor, whereas the widely distributed north temperate genera are relatively species-rich (average = 3.5). The disjunct taxa have a lower species/genus ratio than that extracted from Li (1952) for all of eastern North America (average = 1.9 species/genus, Table 1).

Phylogeny. The distribution of taxa in the phylogenetic categories is highly non-random (Table 3). Disjunct taxa are three times more likely to be "Ranalian" than the total native flora; disjunct taxa contribute 47 percent of all native taxa in this category, although they account for only 13 percent of the flora as a whole. By contrast, only one percent of absent taxa are "Ranalian," whereas 65 percent (the highest of any of the groups) are in the third, most advanced, phylogenetic category. Disjunct taxa are strongly under-represented in the latter category (14 percent of phytogeographic disjuncts are category 3; four percent of all phylogenetic disjunct plants are in category 3). As might be expected, then, Poaceae (Koyama & Kawano, 1964) and Asteraceae are relatively poor in disjunct taxa, but relatively rich in taxa in the absent category (Table 3). Taxa in widely distributed north temperate genera are generally a random selection of the flora as a whole; the only significant departure from a random model is an under-representation in the "Ranalian" phylogenetic category.

AUTECOLOGY

Life history. The disjunct taxa are more strongly perennial (98 percent of all disjuncts) and woody (51 percent of all disjuncts), than the flora as a whole (Table 4). Ninety-nine percent of the annual and 91 percent of the biennial plants are contributed by the non-disjunct phytogeographic categories. The absent taxa are strongly herbaceous (92 percent); except for woodiness, however, these taxa are essentially random samples of the flora as a whole. North temperate taxa are over-represented in the herbaceous category and under-represented in the woody category, but otherwise also are randomly distributed compared to the flora as a whole. Interestingly, the disjunct taxa have a significantly higher percentage of evergreens (eight percent), despite the common observation that disjuncts are associated with deciduous forest landscape.

Growth form and mature height. Disjunct

TABLE 2. Phytogeographical categories in the native flora of Great Smoky Mountains National Park (the distribution of the genera does not sum to 100 percent because of taxa that are disjunct at other than the generic level).

	Taxa (n)	%	Genera (n)	%	Species/ Genus
Absent	232	19	125	29	1.9
Disjunct	162	13	108	25	1.5
North temperate	817	68	231	53	3.5
Native flora	1,211	100	437	100	2.8

taxa are dominantly phanerophytes (42 percent) and geophytes (33 percent); these percentages are higher in the disjunct category than in any other phytogeographic category (Table 5). By contrast, taxa belonging to genera absent from eastern Asia are dominantly hemicryptophytes (54 percent) and have a relatively low percentage of phanerophytes (seven percent). The absent taxa are over-represented in therophytes (25 percent) and geophytes (25 percent), whereas the disjunct taxa are over-represented in the phanerophyte (33 percent), chamaephyte (40 percent), and geophyte categories (23 percent).

Disjunct taxa have a higher percentage distribution in the taller height classes (34 percent of all disjunct taxa reach at least 4 m in height; 55 percent of all plants surpassing 4 m in height are disjunct taxa) than any other floristic category (Table 5). Most taxa absent from eastern Asia are in the smaller height classes (95 percent reach less than 2 m tall), and this phytogeographical category makes its strongest contribution to the flora in the smaller sizes (Table 5).

Phenology and flower color. Seventy-two percent of the disjunct taxa bloom in spring and less than one percent in autumn (Table 6). The peak flowering time for absent taxa is summer (58 percent). Percent contribution to the phenologic periods also reflects this: disjunct taxa make their strongest contribution to the spring flora (22 percent), whereas absent taxa make their peak contribution to the aestival flora (29 percent). Flower color is also skewed: the most important color for disjunct taxa is white (44 percent of all disjunct taxa). White is also the most important flower color for absent taxa (28 percent), but that group has the highest percentage yellow (23 percent) and blue-purple (19 percent) flowers of any floristic category and makes a relatively strong total contribution to those categories (30 percent of all yellow and 34 percent of all blue-purple flowered taxa are absent from eastern Asia—the yellow-flowered taxa occur mostly in the Asteraceae, a family poor in disjunct taxa, as noted above).

Disjunct taxa also have a significantly ($P <$

TABLE 3. Distribution of taxa in phylogenetic and phytogeographical categories (see text for an explanation of the groups). The random model in Part A below is percentage of native taxa in the phylogenetic category; in Part B it is the percentage of the phytogeographic category in the flora as a whole. ** = $P < 0.01$; + = $P <$ 0.001; ++ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Phylogenetic Categories			Poaceae n = 92	Asteraceae n = 138
			1 n = 62	2 n = 534	3 n = 545		
A. Distribution within phytogeographic categories:							
Absent	232		1+	34**	65++	9 ns	20++
Disjunct	162		19++	67++	14++	2**	2++
North temperate	817		5 ns	47 ns	48 ns	8 ns	11 ns
Native flora	1,211		6	46	48	8	11
B. Distribution within phylogenetic categories:							
Absent		19	3++	15**	28**	22 ns	34++
Disjunct		13	47++	20+	4++	3**	2++
North temperate		68	50+	65 ns	68 ns	75 ns	64 ns

TABLE 4. Distribution of taxa in life history and phytogeographic categories (see text for an explanation of the latter). The random model in Part A below is the percentage of native taxa in the life history categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = $P < 0.05$; ** = $P < 0.01$; + = $P < 0.001$; ++ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Life History			Woodiness		Deciduousness	
			Perenn. n = 1,045	Annual n = 131	Bienn. n = 35	Woody n = 246	Herbac. n = 965	Decid. n = 1,137	Evergreen n = 74
A. Distribution within phytogeographic categories:									
Absent	232		83 ns	14 ns	3 ns	8++	92++	96 ns	4 ns
Disjunct	162		98++	1++	1++	51++	49++	92 ns	8*
North temperate	817		85 ns	12 ns	3 ns	28 ns	82 ns	94 ns	6 ns
Native flora	1,211		86	11	3	20	80	94	6
B. Distribution by life history:									
Absent		19	18 ns	25*	20 ns	7++	22++	20 ns	12 ns
Disjunct		13	15*	1++	9 ns	33++	8++	13 ns	20 ns
North temperate		68	67 ns	74 ns	71 ns	60*	70*	67 ns	68 ns

TABLE 5. Distribution by growth form and phytogeographic category (see text for an explanation of the latter). The random model in Part A below is the percentage of native taxa in the life history categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = $P < 0.05$; ** = $P < 0.01$; + = $P < 0.001$; ++ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Raunkiaer Class					Height when Mature (m)				
			Phaner. n = 235	Chamae. n = 10	Hemi-crypt. n = 605	Geo. n = 229	Thero. n = 132	<1 n = 799	1–2 n = 212	2–4 n = 76	4–8 n = 21	>8 n = 103
A. Distribution within phytogeographic categories:												
Absent	232		7++	0.4 ns	54 ns	24*	14 ns	72++	23*	3*	0.4**	1++
Disjunct	162		47++	3 ns	16++	33+	11++	44++	9++	12**	9++	25++
North temperate	817		17 ns	0.6 ns	56**	15**	12 ns	69 ns	18 ns	6 ns	0.6**	7*
Native flora	1,211		19	0.8	50	19	11	66	17	6	2	9
B. Distribution by growth form:												
Absent		19	7++	10 ns	21 ns	25*	25*	20 ns	25*	9**	5*	3++
Disjunct		13	33++	40*	4++	23++	2++	9+	7+	26**	71++	39++
North temperate		68	60*	50 ns	75++	52++	73 ns	71*	68 ns	65 ns	27++	58*

TABLE 6. Distribution by phenology, flower color, and phytogeographic category (percentages by phenology do not sum to 100 because some plants bloom throughout the year). The random model in Part A below is the percentage of native taxa by floral categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = < 0.05; ** = P < 0.01; + = P < 0.001; ++ = P < 0.0001; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Phenology				Flower Color						
			Vernal n = 79	Late Vernal n = 562	Aest. n = 467	Autumn. n = 77	Brown n = 21	Green n = 343	Blue-purple n = 130	Pink-Red n = 91	Orange n = 13	Yellow n = 178	White n = 365
A. Distribution within phytogeographic categories:													
Absent	232		4**	33++	58++	4 ns	2 ns	15++	19++	11 ns	2 ns	23**	28 ns
Disjunct	162		14++	58**	27+	0.6**	7++	27 ns	4**	9 ns	0.7 ns	9**	44+
North temperate	817		6 ns	48 ns	35**	8**	6**	36++	11 ns	7 ns	1 ns	15 ns	31*
Native flora	1,211		7	46	39	6	2	30	11	8	1	16	32
B. Distribution by floral characteristics:													
Absent		19	13 ns	13++	29++	13 ns	24 ns	10++	34++	28**	31 ns	30++	18 ns
Disjunct		13	28++	16*	9**	1+	52++	13 ns	5**	14 ns	8 ns	8**	19**
North temperate		68	59*	71 ns	62**	86+	24++	77++	61*	58*	61 ns	62 ns	63*

TABLE 7. Distribution by habitat and phytogeographic categories (see text for an explanation of the latter). The random model in Part A below is the percentage of native taxa in the life history categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = P < 0.05; ** = P < 0.01; ++ = P < 0.0001; ns = not significant at the 0.05 level.

| Phytogeographic Categories	Total Taxa (n)	% Native Flora	Habitat (Substrate) Categories				Habitat Openness		
			Terrestrial n = 932	Wetlands n = 230	Rock Outcrops n = 36	Epiphytic n = 13	Forest n = 488	Intermed. n = 396	Open n = 327
A. Distribution by phytogeography:									
Absent	232		82*	14*	3 ns	0.4 ns	41 ns	34 ns	25 ns
Disjunct	162		91++	8++	1*	0 ns	66++	28 ns	6++
North temperate	817		73**	22*	4 ns	1*	35 ns	33 ns	32*
Native flora	1,211		77	19	3	0.5	40	33	27
B. Distribution by habitat:									
Absent		19	20 ns	14*	19 ns	7 ns	19 ns	20 ns	17 ns
Disjunct		13	15*	5++	4*	0*	22++	12 ns	3++
North temperate		68	65*	81++	77++	93 ns	59++	68 ns	80++
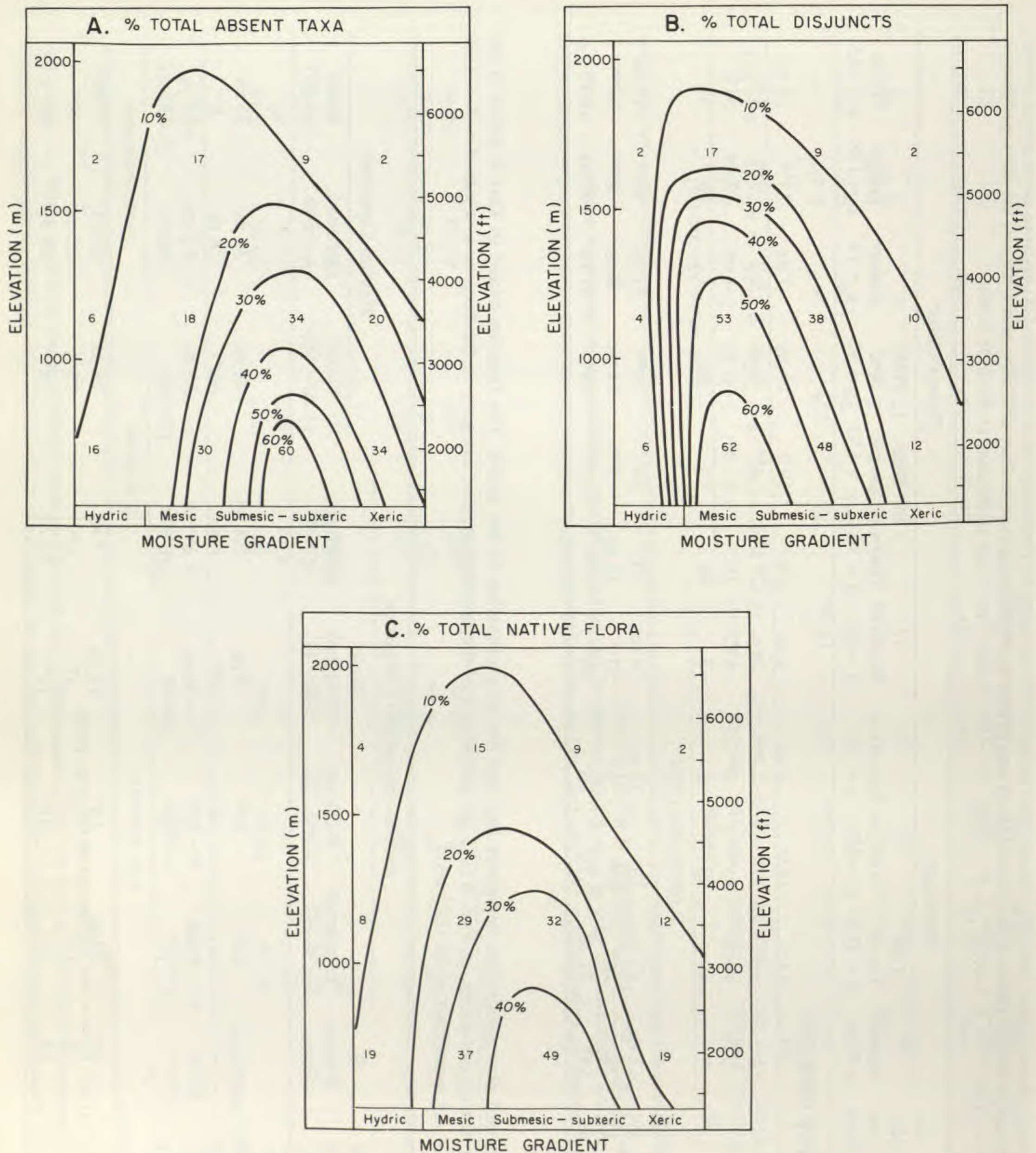
FIGURE 2. Percent distribution of GRSM species along a two-dimensional environmental field. Contours are generalized by ten percent classes; representative data are cited for low, mid, and high elevations and for hydric (wetland), mesic, submesic-subxeric, and xeric sites. A. Absent taxa (232 taxa). B. Disjuncts (162 taxa). C. Total native flora (1,211 taxa).

0.001) earlier peak leaf period (13 percent of all disjuncts and 31 percent of all disjunct herbs have peak leaf periods in spring) than either the absent (eight percent of all taxa, 25 percent of herbaceous taxa have peak leaf periods in spring) or north temperate groups (seven percent of all taxa, 15 percent of herbaceous taxa have peak leaf periods in spring). However, for all phytogeographical categories the peak leaf period is dominantly summer (no significant differences from the total native flora value of 85 percent are found).
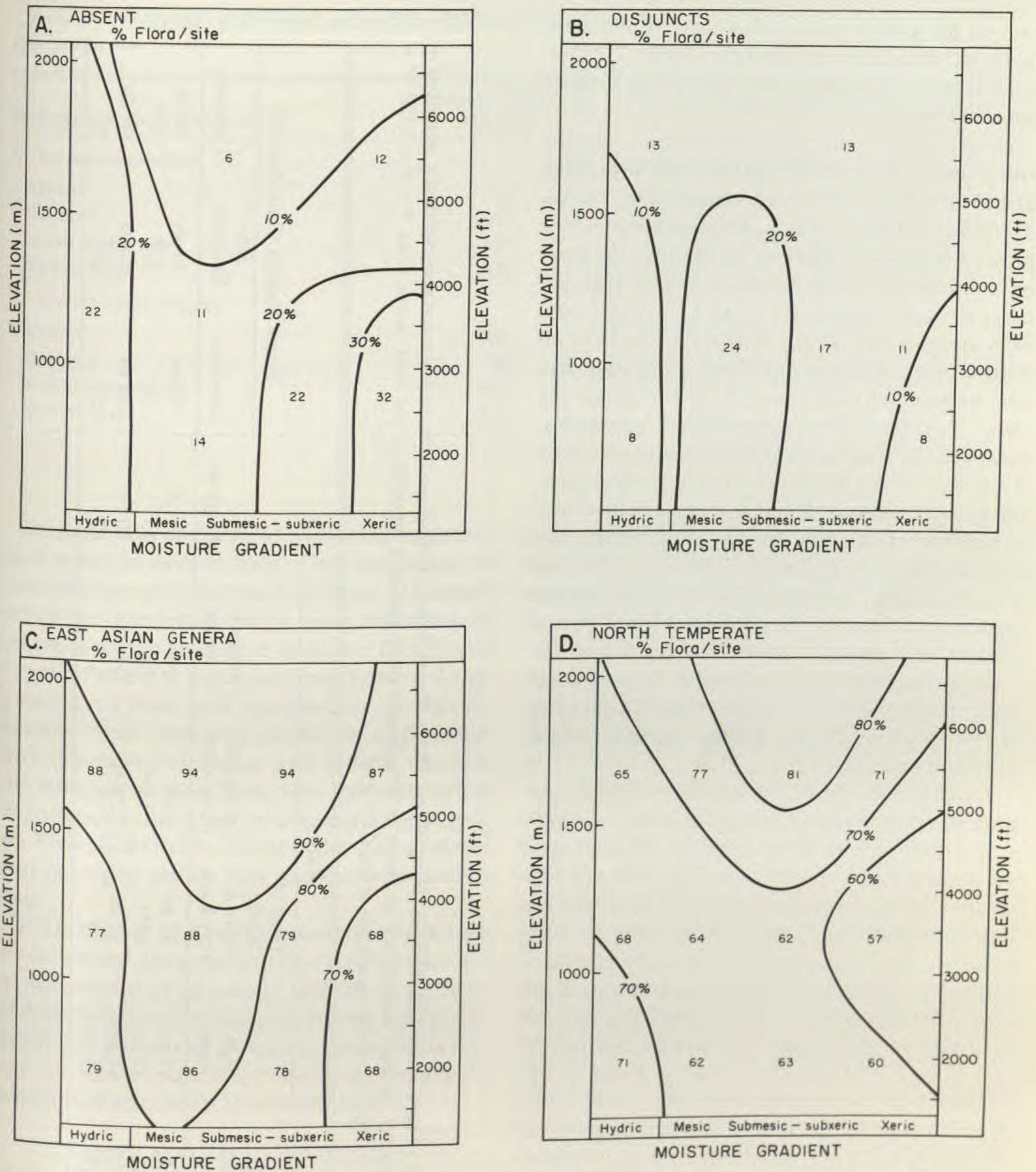
FIGURE 3. Percent contribution of GRSM species to the total expected flora as a function of site. Contours are generalized by ten percent classes; representative data are for low, mid, and high elevations, and for hydric (wetland), mesic, submesic-subxeric, and xeric sites. These diagrams correct for the general decrease of species richness as seen in Figure 2A. A. Absent taxa (232 taxa). B. Disjuncts (162 taxa). C. North temperate taxa (817 taxa). D. All East Asian genera (979 taxa). Only forested sites are shown (see text).

SYNECOLOGY: HABITATS AND GRADIENT DISTRIBUTIONS

Habitat. The disjunct taxa are predominant-ly plants of terrestrial (91 percent of all disjuncts) and forested (66 percent of all disjuncts) habitats. In both cases this is a significant departure from

a random distribution (Table 7). Absent taxa are also over-represented in terrestrial habitats, but are otherwise more or less a random sample of the flora as a whole. Plants of open and wetland habitats dominantly belong to wide-ranging north temperate genera. Despite the fact that the GRSM landscape is heavily forested (99 percent), 27 per-

cent of the park's native plants are found only in open, non-forested habitats (Table 7). Disjunct taxa are strongly under-represented in these open habitats.

Distribution on environmental gradients. Both absent taxa and disjunct taxa have distribution peaks at low elevations (Fig. 2A–B). The disjunct taxa, however, are displaced toward mesic site classes, whereas the absent taxa peak on submesic to subxeric sites. Absent taxa are more strongly represented at the hydric and xeric extremes (16 and 34 percent, respectively of all absent taxa), whereas numbers of disjunct taxa decline more strongly away from the mesic site class. For both phytogeographical categories, however, the total percent decline with elevation is similar—from about 60 percent of the total in the floristic group to about two percent from low to high elevations (Fig. 2A–B). These trends parallel the diversity patterns of the native flora as a whole (Fig. 2C), but here the diversity decline is somewhat less steep (it declines from 50 to two percent with elevation). The distribution of the total native flora is similar to that of the absent taxa, in that there is a submesic-subxeric peak at low elevations and a gradual decline toward moisture extremes.

Two simplifications are possible to better contrast the three floristic groups in terms of landscape distribution. First, because disjunct taxa are unimportant on open sites (*Liriodendron* is an interesting exception), the data base was reduced to plants of forested sites only. Second, because the overall species richness gradient parallels that of the separate phytogeographic groups (Fig. 2A–C), the data were expressed as a percent contribution to the total flora expected on a given site (Fig. 3A–D). In this manner, most of the information on disjuncts available in the 3-dimensional array (elevation, site moisture, habitat openness) is portrayed in two dimensions.

When the data are expressed in this way, the absent taxa show a peak importance in xeric sites, a secondary peak in hydric sites, and a trough in mesic sites (Fig. 3A). Disjuncts show a very different distribution–their peak importance is on mesic sites (Fig. 3B). Taxa of wide-ranging north temperate genera show yet a third pattern, with peak importance at high elevations (the only group to show such an increase with elevation; Fig. 3C). The north temperate taxa are least important on xeric low- to mid-elevation sites; these taxa have a secondary peak on hydric sites.

TABLE 8. Rarity and distribution of taxa in the GRSM flora (from White, 1982). Plants found "throughout" the park are not geographically restricted in the park as a whole. The random model assumes distribution in rarity or distribution categories as a function of the total native flora. * = $P < 0.05$; ** = $P < 0.01$; + = $P < 0.001$; ++ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographical Category	Total Taxa (n)	Rarity				Throughout	Single Habitat Class Records		
		Park Rare	Total of Scarce, Rare & Very Rare	Infrequent-Occasional	Frequent-Common		Elevation	Site Moisture	Openness
Absent	232	18 ns	32 ns	40++	28+	59 ns	50 ns	57 ns	66 ns
Disjunct	162	15 ns	24**	14++	62++	75*	57+	53*	72*
North temperate	817	14 ns	37 ns	28 ns	35 ns	60 ns	53 ns	62 ns	67 ns
Native flora	1,211	15	34	27	37	62	50	60	67

TABLE 9. Narrowly distributed and widely distributed species and an index of beta diversity for two broad-scale gradients.

Phytogeographical Category	Narrowly Restricted Species	Widely Distributed Species	Species Turnover Ratio
A. Elevation gradient:			
Absent	115	127	0.9
Disjunct	60	102	0.6
North temperate	429	388	1.1
Native flora	604	607	1.0
B. Site moisture classes:			
Absent	133	95	1.4
Disjunct	86	76	1.1
North temperate	505	312	1.6
Native flora	724	487	1.5

Disjunct taxa and taxa of wide-ranging genera both occur in eastern Asia. The importance of these two groups is summed in Figure 3D, which shows the percent of forest flora belonging to genera common to eastern Asia as a function of elevation and site moisture class. Eastern Asian genera have their peak distribution on high elevation mesic sites and decline in importance with decreasing elevation and toward extreme site moisture classes. Xeric sites have the lowest importance in distribution of eastern Asian genera. Overall, 85 to 95 percent of the taxa on mesic sites belong to genera that also occur in eastern Asia.

If life history and environmental distribution are combined, these patterns are reinforced. Forty-two percent of all woody taxa on mesic low- to mid-elevation forested sites belong to disjunct genera; 95 percent of all woody plants on mesic low- to mid-elevation forested sites belong to genera that also occur in eastern Asia.

RARITY AND PARK DISTRIBUTION

The phytogeographic categories were contrasted in rarity and park distribution in order to gauge the effect of sporadic distributions on the richness gradients as a whole (Table 8). Disjunct taxa have a lower percent rarity, both in terms of the rarest elements of the park flora and the sum of very rare, rare, and scarce plants. Disjunct taxa are over-represented among frequent and common plants. Disjunct plants are also well-distributed throughout the Smokies (75 percent of all disjuncts are found throughout the park, the highest percent of any of the phytogeographic

groups). The absent taxa are generally a random sample of the flora as a whole, but intermediately common taxa are over-represented and common taxa are under-represented.

Another aspect of distribution breadth was also analyzed: the phytogeographical categories were contrasted in the percentage of taxa restricted to single habitat classes along the three dominant environmental gradients. Two of these gradients were already coded as broad habitat classes: site moisture class (hydric, mesic, submesic-subxeric, xeric) and habitat openness (forested, intermediate, open). Elevation data were summarized in three belts: low (260–760 m; 850–2,500 ft), mid (760–1,370 m; 2,500–4,500 ft), and high (1,370–2,021 m; 4,500–6,621 ft). The results show that disjunct taxa are narrowly distributed along only one of the gradients: habitat openness (Table 8), as noted earlier. In other ways (elevation, site moisture class), the disjunct taxa are less restricted to habitat classes than would be expected based upon chance alone. The other phytogeographic categories are essentially random samples of the flora as a whole in terms of habitat restrictions (Table 8).

The data on gradient restrictions were also used for an index of gradient (beta) diversity. The number of species replacements between the habitat classes (the number of new restricted species encountered in each habitat class) was compared to the number of widely distributed taxa (Table 9). The north temperate taxa have the highest species turnover ratio, whereas the disjunct taxa have the lowest. All phytogeographic categories have higher turnover ratios for

the site moisture class gradient compared to the elevation gradient.

DISCUSSION

Taxa belonging to disjunct genera in GRSM are clearly a non-random sample of the native flora: they are much more likely to be perennial, woody, primitive or intermediate in phylogenetic terms, and earlier in blooming and leafing. Disjunct herbaceous taxa are more likely to be geophytes than are non-disjunct taxa. The taxa belonging to disjunct genera are also non-randomly distributed among habitats—they are more likely to be found on terrestrial, forested, and mesic sites than are non-disjunct taxa. Disjunct taxa are generally more common and more widely distributed in the park than their non-disjunct counterparts.

Unexpectedly, taxa belonging to genera absent from eastern Asia proved just as interesting as the disjunct taxa. For many attributes they also are a non-random assortment of the flora as a whole: absent taxa are more advanced in phylogenetic standing, more herbaceous, less apt to be phanerophytes, shorter in mature height, later blooming (with a stronger representation of yellow flowers), and later leafing. Absent taxa are, however, essentially a random sample of the flora as a whole with regard to substrate and habitat openness. Absent taxa also parallel the whole native flora in gradient distribution: they show a peak occurrence in low elevation submesic-subxeric sites. When the gradient patterns are corrected for the overall distribution of species richness, absent taxa have their peak importance on xeric sites where they make up 20–35 percent of the flora. McVaugh (1943) found that xeric site species (on southeastern United States granite outcrops) had strong phytogeographical ties to western North America. Although the xeric sites analyzed in GRSM are dominated by pine forests, rather than open outcrop communities, the pattern is similar. The taxa of genera absent from eastern Asia are often ones with southwestern United States relatives.

These facts support earlier observations on prominent features of the disjunct taxa: their woodiness (Li, 1952; Wood, 1972), primitiveness (Li, 1952; Sharp, 1953), and habitat distribution (Cain, 1943). Further, there is a clear relationship between life history traits and habitat. Early leafing, geophytic, herbaceous plants are adapted to mesic deciduous forests; in this way

the disjunct taxa parallel the gradient distribution of life history traits in the Southern Appalachians as a whole (Thomas Givnish, pers. comm.). The importance of large phanerophytes is also related to habitat: mesic, low- to mid-elevation forests have the largest biomass of any GRSM communities. The importance of phanerophytes in favorable environments is one of the broad-scale generalizations of the geography of life forms.

Several inferences concerning the contribution of disjunct taxa to the pattern of species richness in the GRSM landscape can be made from these data. Disjunct taxa do not contribute to the several kinds of gamma (whole landscape) diversity. Disjunct taxa are unimportant in open, disturbance-produced habitats. They are relatively frequent plants with uniform distributions throughout the park. They do not increase GRSM richness through occurrence in rare habitats; neither are they rare in common habitats. As a component of the flora, they make no disproportionate contribution to landscape richness per se: they are not patchily distributed.

Disjunct taxa are also relatively unimportant in their contribution to species turnover along gradients (beta diversity). Disjunct taxa decrease more sharply in richness along gradients than the flora as a whole. They do not disproportionately increase richness on extreme moisture class sites or at high elevations (where total diversity is relatively low). Individual taxa are not more narrowly distributed on gradients than non-disjunct taxa, except for habitat openness. The strong inference is that disjunct taxa do not have a higher turnover of taxa along gradients than the flora as a whole, and do not contribute disproportionately to beta diversity.

The disjunct plants are, however, concentrated in mesic low- to mid-elevation forests. These are relatively species-rich habitats for the GRSM landscape as a whole. The contribution of disjunct plants to species richness, then, is non-random in the landscape: from the data presented here, the inference is that this contribution is to alpha (within community) richness. It was, in fact, the concentration of Arcto-Tertiary plants in mesic low- to mid-elevation forests that led Cain (1943) to infer 60 million years of stasis in Southern Appalachian vegetation (since refuted, Delcourt & Delcourt, 1979, 1981). One can summarize the Smokies pattern: disjunct taxa increase the richness of communities that are relatively rich in non-disjunct taxa. This contri-

bution is habitat concentrated, rather than diffused across the landscape or along gradients.

These conclusions only can be extended beyond the study area with caution, however. Only 60 percent of Wood's (1972) disjunct or discontinuous genera occur in GRSM. For all disjunct genera, Li (1952) reported a higher species/genus ratio than that reported here. This is true for North American species of these genera (1.9 species/genus vs. 1.5 for the Smokies) as well as for eastern Asian species, as discussed earlier. Thus, there are, on the continental scale, additional genera and species in eastern North America not accounted for by the GRSM model of species richness. Finally, if the eastern Asian flora was less affected by Pleistocene changes than that of eastern North America (Delcourt & Delcourt, 1979, 1981), there are implications for distribution of species richness. Less environmental change might leave ecological barriers to migration intact and might pose less of a threat to rare, patchily distributed species. These questions will be resolved only as quantitative data become available from the temperate deciduous forests of eastern China, the richest such forests on earth.

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